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1                   **Cameras and carcasses: history and current methods**  
2                   **using artificial food falls for the study of deep-water animals**

3                   Running title: Deep-water animals at food-falls

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8  
9                   **ABSTRACT**

10                   Deep-ocean animals remain poorly understood compared to their shallow-water relatives,  
11                   mainly because of the great cost and difficulty involved in obtaining reliable ecological  
12                   data. This is a serious issue as exploitation of deep-water resources progresses without  
13                   sufficient data being available to assess its risks and impacts. First described almost 40  
14                   years ago, the use of baited cameras was pioneered by deep-sea biologists and is now a  
15                   widely used technique for the assessing patterns of animal behavior, abundance and  
16                   biodiversity. The technique provides a non-destructive and cost-effective means of  
17                   collecting data, where other techniques such as trawling are difficult or impractical. This  
18                   review will first describe the evolution of baited camera techniques in deep-sea research  
19                   from the early deployments, through recent programs to investigate trends in animal  
20                   distribution with depth, latitude, and ocean basin. In the second section the techniques  
21                   used for imaging, baiting, and analysis are synthesized, with special consideration for the  
22                   modeling techniques used in assessing animal abundance and biomass.

23  
24                   ASFA keywords: deep-water, scavengers, marine technology, underwater cameras,  
25                   literature review, fisheries, stock assessment, environmental assessment

## INTRODUCTION

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Baited camera deployment is a deceptively simple technique for the study of the marine environment. Simple because at its most basic level it requires only a time-lapse camera and bait held in its field of view, but deceptive because the view of the marine environment is small and the events seen are artificial. The great advantage of baited systems is that a deployment at a single site aggregates animals from a large distance around it, allowing the animals to be identified, counted, and measured. Diverse and fascinating deep-ocean scavenger communities have been revealed by such cameras and technical and scientific advances continue to improve their usefulness. The technical improvements that allow more effective deep-water research have progressed alongside similar developments in the oil and gas, and fishing industries, bringing the threat of overfishing and habitat destruction to deep-water communities. With these dangers and the discovery of fragile habitats such as cold water coral reefs, effective deep-ocean survey and monitoring tools will become increasingly necessary.

The authors have used baited cameras for much of their work, collecting ecological, behavioral, and physiological data and much of the material presented is from these projects and those of our immediate collaborators. It is the aim of this review to highlight the key historical advances in baited camera research and describe some of the discoveries made in baited camera surveys worldwide. This review will also illustrate the general advantages and disadvantages of baited cameras and then focus on different approaches to imaging, baiting and data interpretation.

1 **PART 1- HISTORY**

2 Baited cameras have now been deployed worldwide, to the greatest depths of the world  
3 ocean, but with a bias towards the US and European ocean margins. From the first baited  
4 camera experiments the majority of studies have been undertaken with systems mounted  
5 on free-falling autonomous vehicles (also known as landers, or pop-up vehicles). These  
6 vehicles consist of a frame, on which the camera system is mounted, and a buoyancy unit.  
7 The system is ballasted, usually with steel scrap, to make it negatively buoyant. The  
8 lander is then deployed by dropping it from the crane or A-frame of a ship, sinks to the  
9 seafloor and takes photographs or video at pre-set intervals. At the end of the experiment  
10 the ballast is dropped by the lander, usually on receipt of an acoustic command from the  
11 surface, and the lander is brought to the surface by the buoyancy unit.

12  
13 Camera and current meter data are then retrieved from the lander, batteries are recharged  
14 or replaced, and the lander is prepared with new ballast and bait for the next deployment.  
15 The use and advantages of autonomous vehicles have been reviewed by Priede and  
16 Bagley (2000) and Bagley et al (2004). These authors particularly highlighted the great  
17 time and cost savings associated with the use of landers, allowing the deploying vessel to  
18 do other work while the lander is in the water (Table 1). In some applications lander  
19 systems can be left *in situ* for months or even years. More recently, a number of other  
20 studies have been conducted by sinking carcasses and periodically visiting them with  
21 Remotely Operated Vehicles (ROVs) or submersibles (Smith 1985), by manually placing  
22 camera systems and bait on the seafloor using these vehicles (Widder et al. 2005), or by  
23 baiting the ROV itself (Tamburri et al. 2000, Trenkel et al. 2004). The variety of vehicles

1 used to deploy cameras, and the range of buoyancy, ballast and release mechanisms is  
2 great and worthy of a review in itself (e.g. Jamieson 2004). This paper, however,  
3 concentrates on scientific payloads, analyses, and the results achieved. A selection of key  
4 lander systems and experiments are highlighted in Table 2.

5

6 *First steps, Isaacs and the “Monster Camera”*

7 The first photographic lander was developed by Ewing and co-workers in the 1940s  
8 (Described in Ewing et al. 1967), and was used primarily for the study of seabed features  
9 such as sand ripples. The first deep-sea baited camera was developed by Isaacs (1969) at  
10 Scripps Institution of Oceanography (University of California, San Diego). Known as the  
11 “Monster Camera” (Fig. 1), this 7000 m rated lander system was deployed in the North  
12 Pacific at depths of up to 5835 m (Heezen & Hollister 1971, Dayton & Hessler 1972).  
13 Later surveys in the Pacific, Indian, and Southern Oceans demonstrated the widespread  
14 presence of an abundant and active scavenging fauna, with fish arriving at the bait in less  
15 than 30 minutes in most deployments (Isaacs & Schwartzlose 1975). Amongst the  
16 animals observed off Baja California were a sleeper shark at 2039 m (Heezen & Hollister  
17 1971) and sablefish, grenadiers, and hagfish at 1400 m (Isaacs 1969). Isaacs (1969)  
18 suggested that some apparently Arctic species, such as sleeper sharks and sablefish, were  
19 really deep-water animals which merely “outcrop” at high latitude where cold water is  
20 close to the surface. Having shown evidence that deep-sea scavengers were abundant,  
21 Isaacs and Schwartzlose (1975) speculated that deep-ocean scavengers use odor plumes  
22 to find bait, and noted that differences in overlying productivity affected both the  
23 numbers of animals attracted and their apparent level of hunger and interest in the bait.

1  
2 The observation of large numbers of active scavengers contributed to the ongoing  
3 controversy over the role of habitat complexity in supporting the observed diversity of  
4 deep-ocean species (Dayton & Hessler 1972, Grassle & Sanders 1973). Controversy on  
5 this matter raged for years, with various authors presenting contrary findings about the  
6 abundance and significance of carrion items as part of a habitat mosaic, and disagreeing  
7 over the significance of scavengers in deep-ocean habitats (Reviewed in Stockton &  
8 DeLaca 1982). Baited cameras are one of the few ways to study deep-water scavengers,  
9 as natural food falls in the deep-ocean are seldom seen (Stockton & DeLaca 1982).  
10 Wilson and Smith (1984) made several important contributions to understanding the role  
11 of scavengers by using the Free Vehicle Video (FVV) system to study the behavior of  
12 foraging abyssal grenadiers. Later, a modified version of this lander was used to make  
13 detailed measurements of the swimming speeds of scavenging amphipods (Wilson &  
14 Smith 1984, Laver et al. 1985). These studies provided key insights into the foraging  
15 methods of deep-ocean scavengers and led to first detailed descriptions of proposed  
16 energetic strategies. These, and following, studies quickly showed that deep-water  
17 scavengers possessed particular energetic characteristics, in particular low routine  
18 metabolic rates (Seibel & Drazen in press). Our understanding of deep-water animal  
19 energetics remains poor, and is a significant limitation to modeling their foraging  
20 behavior. As well as collecting these biological data, Wilson and Smith (1984) also made  
21 the first explicit link between the arrival rates of animals at cameras and the numbers of  
22 those same species caught by trawls in similar locations.  
23

1 *The search for spatial and temporal patterns*

2 Researchers in the UK began two major series of baited camera experiments which  
3 continue to widen the spatial range covered. The main areas of investigation have been  
4 to determine how depth and overlying productivity affect community composition, and  
5 how scavenger communities differ between ocean basins.

6  
7 The landers used were a baited version of the Institute for Oceanographic Sciences  
8 Bathysnap system (Lampitt & Burnham 1983), and the Acoustic Tracking Experiment  
9 (ATEX) (Priede & Smith 1986). Bathysnap is a “free-fall camera and current meter  
10 system” and differed from many of the systems that preceded it by resting directly on the  
11 seafloor, with the camera facing outwards at a downward angle. Usually deployed as an  
12 unbaited time lapse photography system, the history of Bathysnap has been reviewed by  
13 Bett (2003). The initial baited (or Bathysnack) experiment, at 4009 m in the North East  
14 Atlantic, used the flesh of abyssal grenadiers (*Coryphaenoides armatus*) caught at the  
15 same depth. The bait was wrapped in fine cotton gauze, and attracted amphipods and  
16 fishes (but not large grenadiers) (Lampitt et al. 1983). A key finding was that changes in  
17 current direction and velocity had powerful effects on the numbers of animals seen at the  
18 bait, as Wilson and Smith (1984) observed using the FVV in the Pacific.

19  
20 The first ATEX lander consisted of the FVV fitted with an acoustic tracking module and  
21 was deployed in the North Pacific in 1985 (Priede & Smith 1986). ATEX, and the  
22 subsequent AUDOS and ROBust BIODiversity (ROBIO) landers (Fig. 2), have since been  
23 deployed worldwide to depths of up to 5900 m. Members of this family of vehicles

1 consist of a time-lapse stills or video camera facing downwards from a frame moored 2 m  
2 above the seafloor, kept in tension by the lander's buoyancy (Fig. 2). The majority of  
3 ATEX and AUDOS models included an acoustic system capable of tracking ingestible  
4 transponders. These transponders were hidden in bait packages, and once eaten, allowed  
5 the subsequent movements of the fish to be recorded at pre-selected time intervals  
6 (usually each minute) to a range of 500 m (Bagley *et al.* 1994). Unlike previous landers,  
7 the ATEX was baited with a single fish carcass, which was open to the scavengers. As  
8 the bait was consumed, the scavengers dispersed, allowing the processes involved in  
9 optimal foraging to be studied in the deep-ocean for the first time. Arrival rates, staying  
10 times, and swimming speeds were determined for a range of scavenging fishes, allowing  
11 greatly-improved estimates of scavenger abundance to be made. A key finding was that  
12 abyssal grenadiers appeared to move slowly but continuously, with a bias towards cross-  
13 current movement, and often left the bait while some of it remained unconsumed (Priede  
14 *et al.* 1991). This finding linked to Charnov's (1976) theories on optimal foraging,  
15 which showed that animals should leave a food patch once feeding opportunity at the  
16 patch dropped below the average level for the environment as a whole. A key question  
17 was whether differences in abyssal scavenger staying time could be linked to differences  
18 in the surface productivity of the overlying waters.

19

20 **Latitude and surface productivity.** The great majority of primary productivity in the  
21 ocean occurs close to the surface, which in turn provides food to the underlying deep-  
22 water habitats. Spatial variation in surface productivity directly influences the amount of  
23 food reaching the seafloor as particulate organic matter (Smith *et al.* 1997b), and

1 potentially affects the amount of carrion produced by the shallow-water nekton  
2 populations. When deployed along a transect in the North Atlantic, bathysnap revealed a  
3 fish-dominated system on the Porcupine Abyssal Plain (southwest of Ireland) with  
4 apparent fish abundance and size decreasing to the Madeira Abyssal Plain in the south  
5 (Merrett 1987). These findings and trawl data led to the theory of a zoogeographic divide  
6 at 40°N. This theory stated that there was a lower biomass, consisting of small fish  
7 species, in the sub-tropics where productivity was lower and more continuous, compared  
8 to the more productive and seasonal temperate zone (Merrett 1987). When AUDOS was  
9 deployed in the abyssal North East Atlantic it recorded a wide range of scavenging  
10 species, including the grenadier *C. armatus*, the eel *Histiobranchus bathybius*, and the  
11 ophidiids *Spectrunculus grandis* and *Barathrites* sp. (Armstrong et al. 1992). Using the  
12 AUDOS tracking data, abundance estimates were made for the Porcupine Abyssal Plain  
13 (PAP; 167 grenadiers·km<sup>-2</sup> and 180 synphobranchid eels·km<sup>-2</sup>), and Madeira Abyssal  
14 Plain (MAP; 8 grenadiers·km<sup>-2</sup> and 7 synphobranchid eels·km<sup>-2</sup>). As predicted by  
15 optimal foraging theory, staying times were longer at the oligotrophic MAP. These  
16 findings supported the zoogeographic divide hypothesis, but baited camera deployments  
17 and tagging studies further south (Cape Verde Abyssal Plain, 17°N) found elevated  
18 populations of grenadiers (Henriques et al. (2002). These studies showed that the lower  
19 abundances of *C. armatus* off Madeira corresponded with lower surface productivity, but  
20 that the seasonal upwelling system above the Cape Verde Abyssal Plain was capable of  
21 supporting large grenadiers. The surface productivity of an ecosystem could therefore be  
22 linked to the characteristics of its deep-water scavenging fauna.  
23

1 **Depth.** It has long been known that community composition changes with depth, with  
2 species being found in specific depth zones (Grassle et al. 1975). Baited camera  
3 experiments confirmed trawl data showing distinct zonation in deep-sea fishes (Fig. 3).  
4 In the temperate North-East Atlantic, baited camera data were dominated by observations  
5 of the eel *Synaphobranchus kaupii* on the upper slope (to around 1200 m), which were  
6 then replaced by morid cods (*Antimora rostrata*), until at about 2000 m when they were  
7 replaced by the abyssal grenadier (*C. armatus*) (Armstrong et al. 1992, Priede & Merrett  
8 1996, Collins et al. 1999a). Collins et al. (2005) combined trawl and baited camera data  
9 to investigate patterns in the deep-sea fish community with depth. These analyses  
10 showed that, while both biomass and abundance of fishes fell with increasing depth,  
11 patterns in body size differed greatly between scavenging and non-scavenging fishes,  
12 with the scavengers (those species seen at baited cameras) increasing in average mass  
13 with depth. This was explained by a mathematical model of fish foraging which showed  
14 that the optimum body size for fishes depended on characteristics of the meals they  
15 utilized. Scavengers used larger but less frequent food items and larger size provided  
16 scavengers with the endurance necessary to travel between sporadic feeding  
17 opportunities. Differences in energetic strategy between sharks and bony fishes may also  
18 explain differences in the depth distributions of Osteichthyan (bony) and Chondrichthyan  
19 fishes (sharks, rays, and chimaeras). To investigate this phenomenon Priede et al (2006)  
20 collated data for 166 baited camera deployments in the Pacific, Atlantic, and Southern  
21 Oceans, Mediterranean and Arabian seas. These data showed that the entire class  
22 Chondrichthyes is confined to waters less than 3000 m deep. All species in this class are

1 vulnerable to the over fishing which is decimating shark populations (Myers & Worm  
2 2005).

3

4 At the extreme end of the depth range, baited cameras have been used in the ocean  
5 trenches, to depths in excess of 10 km. The deepest recordings of fish were of grenadiers  
6 (*Coryphaenoides yaquinae*) at 5900 m (Priede et al. 1990) and brotulids at 5861 m  
7 (Hessler et al. 1978) in the North and South Pacific respectively. Deeper deployments  
8 observe only scavenging crustaceans, but often in great numbers (Birstein &  
9 Vinogradov 1955, Beliaev 1989). The true depth limits of fish distribution are not yet  
10 clear, and the mechanisms controlling the distributions of fishes are not known as a wide  
11 range of physical (light, pressure, temperature) and ecological variables (food  
12 availability, numbers of predators) co-vary with depth. Various ecological and  
13 physiological hypotheses have been erected, but none completely explains the data  
14 (Priede et al. 2006).

15

16 **Comparing abyssal basins.** The majority of abyssal (>2000 m) baited camera  
17 experiments have been undertaken in the North Pacific and North Atlantic Oceans. In  
18 both of these oceans the abyssal plain fish community is dominated by large grenadiers.  
19 In the temperate Atlantic the plains species is *C. armatus*, while in the Pacific this species  
20 is confined to the lower reaches of the ocean margins and the plains are dominated by *C.*  
21 *yaquinae* (Wilson & Waples 1983). The Atlantic temperate fauna is well characterized  
22 and found consistently across a wide area, but the northern and eastern extensions of this  
23 ocean are quite different. Jones et al (2003) described the scavenging fauna of the

1 Mediterranean sea, demonstrating that the large grenadiers and amphipods that dominate  
2 scavenging fauna of the oceanic abyss are absent at similar depths in this enclosed sea.  
3 The abyssal scavenging fauna is numerically dominated by a shrimp, *Acantheephyra*  
4 *eximia* (Jones et al. 2003), which can be found around hydrothermal vents in the Atlantic  
5 (Desbruyères et al. 2001). The much greater water temperatures at depth, shorter time  
6 that the Mediterranean abyss has been habitable, and the shallow sill (<300 msw) which  
7 separates this sea from the Atlantic are all possibly responsible for preventing the entry of  
8 the “normal” oceanic fauna. To the north, above the Arctic circle, grenadiers are also  
9 absent, and the abyssal scavenging fauna is dominated by amphipods (Klages et al. 2001)  
10 and higher up the slope the main scavenging fish are zoarcids (Premke et al. 2003).  
11 Lower temperatures in the Arctic might be a factor, but it is interesting to note that in the  
12 abyssal Arabian Sea zoarcids are also among the dominant scavenging fish species seen  
13 by baited cameras and large grenadiers are very rare (Janßen et al. 2000). Like the  
14 Atlantic, the southern Indian Ocean the abyssal fish community appears to be dominated  
15 by large *C. armatus*. (King 2006).

16

17 **Temporal patterns.** Spatial patterns have been extensively examined, but temporal  
18 patterns are extremely poorly characterized. Seasonal comparisons using acoustic  
19 tracking (Priede et al. 1994b) and video analysis (Priede et al. 2003) showed changing  
20 levels of swimming activity in abyssal fishes, but these could also have been caused by  
21 interannual changes in nutritional state (Drazen 2002). Changes in length frequency  
22 distribution indicated that migrations by grenadiers may have occurred (Smith et al.  
23 1997a, Priede et al. 2003), but confirming this will require much more data.

1

2 **PART 2 - TECHNOLOGY FOR SURVEY AND SCIENTIFIC STUDIES**

3 While deployment methods differ, all systems require a camera, light, and a means of  
4 attracting animals. The choice of each item depends on the specific aims of the  
5 deployments (e.g. from survey to behavioral study), and how well characterized the fauna  
6 is prior to deployment.

7

8 **Camera systems**

9 There are many options to be considered including the sizes and angles of the fields of  
10 view, type of lighting, and between video and still photography. The Bathysnap and  
11 “Eye In The Sea” (Widder et al. 2005) vehicles used oblique photography, providing a  
12 larger field of view, and good side views of the animals, making them potentially easier  
13 to identify than in top-down images. One disadvantage of this technique is that from a  
14 single camera it is impossible to estimate the sizes of animals which are not touching the  
15 seafloor (animals on the bottom can be sized using a “Canadian grid” superimposed on  
16 the image). Oblique angled photography is mainly used for unbaited deep-sea  
17 photography, where most of the animals of interest are on the seafloor (Kaufmann &  
18 Smith 1997, Bett et al. 2001). One other potential disadvantage of baiting an obliquely-  
19 angled camera is that the results obtained may be affected if the camera’s supporting  
20 structure is touching the seafloor. Jamieson et al (2006) recently described how fish often  
21 ignore the bait and investigate lander frames, potentially making them invisible to the  
22 camera for long periods of time. For this reason Jamieson et al (2006) recommended

1 that lander or mooring parts coming close to the seabed should be within the field of view  
2 of the camera.

3

4 The “monster camera” used a downward-looking camera, tethered off the seafloor to  
5 maximize the field of view. This system was adopted in the design of the FVV (and its  
6 descendants ATEX, AUDOS, and ROBIO), using a measured scale bar close the  
7 seafloor. By using this reference length and calculating the range of benthopelagic  
8 animals from the position of their shadows on the seafloor, the lengths of animals can be  
9 calculated from a single camera, even when they are not in contact with the seafloor.  
10 However, the accuracy of the estimates falls dramatically as the animals get further from  
11 the seabed and the reference scale (N.J. King and D.L. Watson, unpublished data). With a  
12 downward-facing camera there is clearly a trade-off between the seafloor area visible and  
13 the amount of detail available in the images, usually determined by the camera’s range  
14 from the seafloor. Placing the camera closer and using a wide-angle lens is an attractive  
15 option but causes measurement artifacts if lengths and swimming speeds are to be  
16 determined from images or video sequences.

17

18 Most baited camera deployments undertaken for survey and census have used stills  
19 cameras, mainly because the increased resolution available from film made species  
20 identification easier. However, recordings of swimming movement from video can also  
21 be used when classifying organisms. Video has been used by several teams to collect  
22 information on locomotory performance and behavior in deep-sea animals. One recent  
23 example is the “Sprint” lander, which used video in conjunction with an electrical

1 stimulator to elicit burst swimming performances from fish and shrimps attracted to bait,  
2 allowing their muscle power output to be estimated (Bailey et al. 2003). Collins *et al.*  
3 (1999a) used video data, alongside acoustic tracking to show how fish activity levels are  
4 reduced at greater depths, probably as a consequence of lower food availability.

5

6 Current high-resolution, color video cameras, require relatively large amounts of light.  
7 For example the Sprint lander used twin 75 W incandescent lamps (Bailey et al. 2003).  
8 Long periods of illumination at such light intensities sometimes affect the behavior of the  
9 animals that the camera is there to observe. The bathyal eel *S. kaupii* (Bailey et al. 2005)  
10 slowly moved away from the camera field of view when lit, but the abyssal grenadier *C.*  
11 *armatus* did not avoid the lights used to illuminate it (Wilson & Smith 1984). Recent  
12 studies suggest that *S. kaupii* interacts with bioluminescent ostracods during scavenging  
13 (Heger et al. in press), and reacting to their light may be a natural behavior for these  
14 fishes. Other bathyal fishes such as toothfish also react to the lights of video landers  
15 (Collins et al. 1999b), and like the eels, this may be because light has some ecological  
16 relevance to this species, perhaps during a shallower-living point in their life cycle.

17

18 One solution to the lighting problem is to use a high-frequency acoustic camera, to which  
19 the fishes should be completely oblivious, but under most conditions the image quality  
20 and field of view are not as good as those of optical cameras (Rose *et al.* 2005). More  
21 conventional active sonars provide much greater fields of view (Smith et al. 1989b), but  
22 are currently best used in conjunction with cameras (Premke et al. 2003). Camera  
23 systems using red light illumination appear to disturb fish less than those using white

1 light, resulting in greater numbers of scavenging animals, while providing sufficient light  
2 for video recording (Widder *et al.* 2005).

3

#### 4 **Baits and other attractants**

5 After setting up all the high-tech hardware the camera must be baited. This is a critically  
6 important part of the procedure, as small details of the size, type, and configuration of the  
7 bait affect the results obtained. The most common baits are shallow-water fishes, either  
8 in a leaky container or open to the scavengers. In either case scavenging animals are  
9 attracted by the production of an odor plume which stretches downstream of the baited  
10 camera. This is a very cheap and effective means of attracting animals to the camera  
11 from a large area, but suffers from some significant disadvantages. The baits used are not  
12 standardized between research groups, making comparison of results difficult, as the rate  
13 of odor release, and the length of time that the bait lasts depends completely on the type  
14 of fish used (Lampitt *et al.* 1983) and how it is prepared (homogenate, fillets, whole).  
15 The early experiments tended towards enclosed baits, but following Priede and Smith  
16 (1986) many teams now use open baits to mimic small natural food falls. With such open  
17 baits there is a feedback process between the numbers and sizes of the scavengers  
18 attracted and the length of time that the bait remains attractive (Collins *et al.* 2002). This  
19 probably makes the results obtained less consistent between deployments and details of  
20 how the bait is attached to the camera system greatly affect how long it remains visible.  
21 Bait mixes enclosed in a mesh container or released by a pump are probably more  
22 consistent between deployments than whole fish, but the form and duration of the feeding  
23 frenzy produced cannot mimic events at a natural carrion fall. Monterey Bay Aquarium

1 Research Institute researchers used liquidized fish, emitted by a pump, to attract mobile  
2 animals in an experiment to test the effects of deep-ocean carbon sequestration on deep-  
3 living animals (Tamburri et al. 2000). This bait was so effective that the fish remained  
4 present even when the pH of the water around the bait source was reduced from 7.6 to 5.6  
5 by CO<sub>2</sub> hydrate pumped from the ROV. While most researchers use fish in some form as  
6 bait, plant remains have also been used. Traps baited only with sea grass and seaweed  
7 captured amphipods at depths of 10 and 500 m off the Bahamas (Lawson et al. 1993).

8

9 Changing the type and configuration of the bait affects both the numbers of animals seen,  
10 and the species observed. The Bathysnap system observed *Pachycara bulbiceps*, which  
11 was not observed at the same locations by Armstrong et al (1992), but did not observe *C.*  
12 *armatus*, the dominant fish scavenger at that depth. Bathysnap has always used enclosed  
13 baits and tends to be deployed for longer durations than the AUDOS lander with its open  
14 bait (usually a single Atlantic mackerel, *Scomber scombrus*). The greater persistence of  
15 the protected bait allows zoarcids to arrive and exhibit the “roosting” behavior for which  
16 they are now well known (Witte 1999, Janßen et al. 2000, Kemp et al. 2006).

17

18 One disadvantage of small, unprotected baits is that the experiment is over very quickly  
19 (often within hours of lander touchdown), but in a recent development Kemp et al. (in  
20 press) deployed a periodic bait-release system during a long-term lander experiment on  
21 the Mid-Atlantic Ridge. The periodic bait-release contained several individual fish  
22 carcasses in sealed tubes, which were released singly at pre-determined intervals. The  
23 system produced replicate baited experiments, with grenadier fishes apparently leaving

1 the lander after feeding and being attracted when new bait was released. The sealing of  
2 the bait within the tubes, and the deactivation of surface-dwelling microorganisms by the  
3 environmental pressure, appeared sufficient to retain the freshness of the bait between  
4 bait releases. This system has great potential for the study of scavenging animals during  
5 periods when ship operations are impractical, such as during winter at higher latitudes.

6

7 The largest baits used on landers are the carcasses of small marine mammals (Jones 1999,  
8 Kemp et al. 2006), which attract very large numbers of scavenging fishes and  
9 invertebrates for periods of several weeks. Such studies have provided fascinating  
10 information on deep-water ecology and in particular the interactions between species.  
11 For example Kemp et al (2006) showed that changes in numbers of crabs feeding on the  
12 carcass of a porpoise fluctuated violently, but the drops in crab numbers were associated  
13 with the presence of predatory octopods. There have been several studies of large marine  
14 mammal carcasses, made by sinking them into deep water with large weights and then  
15 visiting them periodically with ROVs and submersibles (Smith & Baco 2003). The  
16 succession of animals at whale carcasses, began with a “mobile scavenger” phase, similar  
17 to that seen at baited landers, ending with a “reef” stage when the nutritional content of  
18 the skeleton has been exhausted by sulphophilic organisms and the bones were  
19 colonized by suspension feeders (Smith & Baco 2003). The observation of  
20 chemoautotrophs feeding at whale carcasses led to the “stepping stone” theory, which  
21 suggested that whale carcasses might provide the necessary habitat to support the  
22 dispersal of vent animals from one hydrothermal fluid source to the next (Smith et al.  
23 1989a).

1

2 The above techniques attract animals using an odor plume, and perhaps also with an  
3 acoustic/mechanoreceptor signal from the impact of the carcass on the seafloor (Klages  
4 et al. 2002, Premke et al. 2003). The only alternative artificial attractant of which the  
5 authors are aware is the “electronic jellyfish” developed by Widder and her co-workers  
6 (2005). The “jellyfish” consists of a computer-controlled array of white LEDs which  
7 produces moving patterns of light similar to those produced by a distressed jellyfish. It  
8 appears that this system does attract the attention of predators near the lander, but the  
9 usefulness of this system as a sole means of attracting animals to a camera has not yet  
10 been established. As noted above, scavengers may also utilize mechanoreception to  
11 detect the arrival of carrion on the seafloor, but there has been little experimental testing  
12 of this *in situ*.

13

14 In general terms, video cameras and open, natural, baits have advantages for behavioral  
15 studies, particularly using red light illumination. High resolution digital stills cameras  
16 and enclosed (or at least very standardized) baits are probably better for census purposes,  
17 especially in areas where the fauna has not been characterized by previous photographic  
18 or capture methods (King et al. 2006).

19

20

### **Interpretation of baited camera data**

21 Many systems exist for photographing and videoing the animals attracted to baited  
22 cameras, but how much information can be gleaned from the small area imaged? Baited  
23 cameras are part of a suite of techniques available to deep-sea researchers (see Table 1),

1 but may often be the most practicable survey method. In environments such as reefs,  
2 where trawling would be unacceptably damaging, deployment of baited cameras may still  
3 be possible. Lander deployments also require less ship time and equipment than trawling,  
4 ROV or submersible use, especially at abyssal depths. It is important then that the  
5 distribution patterns and abundance estimates produced by baited cameras are  
6 comparable to those from other methods, and that any systematic differences in the  
7 results obtained should be known.

8

9 **Species composition.** At the simplest level, determination of species presence can be  
10 achieved relatively easily and this work forms the basis of the comparisons between  
11 abyssal basins presented above. It may sometimes be difficult to make good species  
12 identifications from the top-down images collected by baited camera systems  
13 (identification books seldom show a dorsal view), and careful morphometric  
14 measurements from the images may be required to discriminate anatomically similar  
15 species (King 2006). This problem was first noted by Barnes (1955), but the deep-sea  
16 implementation of the baited stereo-camera techniques used by fisheries scientists (Cappo  
17 et al. 2004) is a potential solution. Alternatively, voucher specimens for identification  
18 can be obtained by trawling (if possible) or the deployment of baited traps or hooks.

19

20 Comparisons of the species lists generated by baited camera and trawl censuses often  
21 differ greatly, as baited cameras usually only attract scavengers. In the NE Atlantic only  
22 18 species were attracted to bait compared with 71 species within trawls (Priede et al.  
23 1994a, Priede & Merrett 1996). A recent survey of demersal fish species on the Mid-

1 Atlantic Ridge also observed 22 species at baited landers, 40 species on a series of  
2 thousands of baited long line hooks, and 80 species in Campelen trawls (King et al. 2006,  
3 Fossen et al. in press, submitted). In a recent global comparison, more than twice as  
4 many species were found at any depth with otter trawls (OTSBs) than with baited  
5 cameras (Priede et al. 2006).

6

7 **Calculating animal abundance and biomass.** A more significant challenge than  
8 determining that a species is present is to estimate the true abundances of that species in  
9 the wider environment. The number of animals at the bait changes continuously during  
10 the deployment (Fig. 4), often resulting in a feeding frenzy of fish and crustaceans filling  
11 the camera field of view (Fig. 3). Interpreting these data requires information or  
12 assumptions about the sensory abilities and foraging method of the animals, and the  
13 behavior and area of influence of the odor plume after it has left the camera system.

14

15 The scenario used in the present generation of models is that the odor is carried  
16 downstream by the current and either reaches a stationary animal, or that animal swims  
17 into the odor plume while actively searching for food (Priede & Merrett 1996, Bailey &  
18 Priede 2002). The length and spread of the odor plume (and thus the number of animals  
19 which it contacts) are determined by the current velocity (and so a current meter is  
20 usually fitted to the lander). Upon contacting the odor, rheotaxis is triggered, and animals  
21 use the odor plume gradient to stay within the plume until they reach the baited area.  
22 They then locate the bait, feed until the bait is either consumed, or leave sooner if they  
23 estimate that better feeding opportunities exist elsewhere (Charnov 1976). There are

1 major differences between species in their tendency to remain in the vicinity of baits and  
2 it is very difficult to determine individual staying times unless acoustic tagging is used, or  
3 a fish has an unusual distinguishing feature such as a prominent ectoparasite. The  
4 number of animals at any one time therefore depends on the current velocity, movement  
5 speeds of the animals (which may also be affected by current velocity), and how long the  
6 animal stays at the bait (which is determined by both its feeding rate, the actions of other  
7 animals, the bait characteristics, and the number of other feeding opportunities).

8

9 The earliest abundance calculation model was a “sit and wait” model for crabs, developed  
10 by Sainte-Marie & Hargrave (1987), and subsequently developed by Collins and co-  
11 workers (2002). This latter model used the arrival rate and estimates of effective plume  
12 area to estimate abundance from the arrivals of many animals and is therefore a very  
13 robust measure. These models assume Gaussian odor plume dispersal, that every  
14 individual of the focal species responds similarly to the odor of the bait and that all the  
15 animals attracted remain at the bait throughout the recording. Priede et al (1990)  
16 proposed a simple model for the calculation of fish abundances based on their first arrival  
17 time, and allowing for the dispersal of fish after feeding (Fig. 4C). The model was easy  
18 to implement and produced abundance estimates which were close to those of otter trawls  
19 done at the same locations (Fig 5A) (Priede & Merrett 1996). This model is the basis of  
20 all the abundance estimates for AUDOS and ROBIO deployments described in this  
21 review. In an effort to develop models which described the data more accurately Bailey  
22 and Priede (2002) developed models which allowed for “sit and wait”, “cross current  
23 foraging”, and “drifting” behavior patterns. Although the newer models appeared

1 qualitatively to mimic “real” deployment data more closely, the greatly-increased  
2 difficulty of using them for abundance estimates cannot be justified on the basis of the  
3 available field data. Results from this model are shown in Fig 5B, comparing abundance  
4 estimates from a towed camera sled to those from the Sprint video lander. Careful field  
5 trials, and a statistical analysis of the model predictions will be required to determine  
6 which models are the most appropriate for the analysis of baited camera data.

7  
8 Once abundances have been estimated scavenger biomass can be calculated, using animal  
9 dimensions and allometric relationships. In comparison with trawl data in the NE  
10 Atlantic, landers sampled a more limited size range, not fully representing juveniles and  
11 very large specimens of *C. armatus*. Noting this difference in size frequency led to the  
12 discovery that brain morphology changes throughout life in *C. armatus* as its niche  
13 changes ontogenetically (Wagner 2003).

### 14 15 **Data gaps**

16 There are significant gaps in our understanding of both odor plume and animal foraging  
17 behavior. For instance we know little about the odor sensitivity of deep-sea animals, or  
18 how the odor plume disperses, especially in rough terrain such as reefs and canyons (Fig.  
19 5C). While the AUDOS tracking system has provided much useful behavioral  
20 information, this data could only be collected after the animal had fed (and eaten the  
21 transponder) and therefore could not describe the animals’ previous actions (e.g. its  
22 reaction to the plume). At this time we lack critical information on energetic strategies,  
23 such as which animals remain stationary on the seafloor until contacted by an odor plume

1 (Wilson and Smith's (1984) "sit and wait" strategy), and which animals search across  
2 currents as other authors suggested (Barnes 1955, Priede et al. 1991). Basic sensitivity  
3 analyses have shown how abundance estimates are greatly affected by assumptions  
4 concerning an animal's foraging method (Bailey & Priede 2002) and swimming speed  
5 (Yau et al. 2000), so some of these data gaps will need to be filled if we are to have great  
6 confidence in lander abundance estimates.

7

8

### **SUMMARY**

9 Baited cameras gave us our first view of a diverse, abundant, and active scavenging fauna  
10 in the dark ocean abyss and in many cases deploying baited cameras is still one of the  
11 most effective ways of obtaining biological information from deep water. Worldwide  
12 surveys have shown patterns in scavenger behavior, abundance, and diversity with  
13 latitude, depth, and between oceans. Despite long experience in the use of these camera  
14 systems, many data gaps remain, which make interpreting the images obtained more  
15 difficult. The choice of camera system and bait, and the amount of background  
16 information available about the environment and the focal species, make a great deal of  
17 difference to the success of the data interpretation. All survey techniques have  
18 assumptions. The avoidance and attraction effects of moving survey gears such as trawls,  
19 camera sleds and ROVs are poorly-known for deep-sea animals, affecting their effective  
20 search area in much the same way that errors are caused in baited camera surveys  
21 (Trenkel et al. 2004). Baited cameras have a long history, and with care their deployment  
22 provides an efficient means of studying the distribution, behavior and abundance of deep-  
23 sea animals.

1

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11

#### LITERATURE CITED

- 12  
13 Armstrong JD, Bagley PM, Priede IG (1992) Photographic and acoustic tracking  
14 observations of the behaviour of the grenadier *Coryphaenoides (Nematonurus)*  
15 *armatus*, the eel *Synaphobranchus bathybius*, and other abyssal demersal fish in  
16 the North Atlantic Ocean. *Mar Biol* 112:535-544  
17 Bagley P, Smith A, Priede IG (1994) Tracking movements of deep demersal fishes in the  
18 Porcupine Seabight, Northeast Atlantic Ocean. *J Mar Biol Assoc UK* 74:473-480  
19 Bagley PM, Priede IG, Jamieson AJ, Bailey DM, Battle EJV, Henriques C, Kemp KM  
20 (2004) Lander techniques for deep ocean biological research. *Underwater*  
21 *Technology* 26:3-12  
22 Bailey DM, Bagley PM, Jamieson AJ, Collins MA, Priede IG (2003) In situ investigation  
23 of burst swimming and muscle performance in the deep-sea fish *Antimora*  
24 *rostrata*. *J Exp Mar Biol Ecol* 286/6:295-311  
25 Bailey DM, Genard B, Collins MA, Rees J-F, Unsworth SK, Battle EJV, Bagley PM,  
26 Jamieson AJ, Priede IG (2005) High swimming and metabolic activity in the  
27 deep-sea eel *Synaphobranchus kaupii* revealed by integrated in situ and in vitro  
28 measurements. *Physiol Biochem Zool* 78:335-346  
29 Bailey DM, Priede IG (2002) Predicting fish behaviour in response to abyssal food-falls.  
30 *Mar Biol* 141:831-840  
31 Barnes H (1955) Underwater television and research in marine biology, bottom  
32 topography and geology. *Ocean Dynamics* 8:213-236  
33 Beliaev GM (1989) Deep-Sea Ocean Trenches and their Fauna, Vol. Nauka Publishing  
34 House, Moscow  
35 Bett BJ (2003) Time-lapse photography in the deep sea. *Underwater Technology* 25:121-  
36 127

- 1 Bett BJ, Malzone MG, Narayanaswamy BE, Wigham BD (2001) Temporal variability in  
2 phytodetritus and megabenthic activity at the seabed in the deep Northeast  
3 Atlantic. *Prog Oceanog* 50:349-368
- 4 Birstein YA, Vinogradov ME (1955) Pelagicheskie gammaridy severnoi chasti  
5 Indiiskogo Okeana [The pelagic Amphipods Gammarids of the northern part of  
6 the Indian Ocean]. *Akademija Nauk SSSR, Trudy Instituta Okeanologii* 65:152-  
7 195
- 8 Cappel M, Speare P, De'ath G (2004) Comparison of baited remote underwater video  
9 stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity  
10 in inter-reefal areas of the Great Barrier Reef Marine Park. *J Exp Mar Biol Ecol*  
11 302:123-152
- 12 Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Pop Biol* 9:129-  
13 136
- 14 Collins MA, Bailey DM, Ruxton GD, Priede IG (2005) Trends in body size across an  
15 environmental gradient: a differential response in scavenging and non-scavenging  
16 demersal deep-sea fish. *Proc R Soc London B* 272:2051-2057
- 17 Collins MA, Priede IG, Bagley PM (1999a) *In situ* comparison of activity in two deep-  
18 sea scavenging fishes occupying different depth zones. *Proc R Soc London B*  
19 266:2011-2016
- 20 Collins MA, Yau C, Guillfoyle F, Bagley P, Everson I, Priede IG, Agnew D (2002)  
21 Assessment of stone crab (Lithodidae) density on the South Georgia slope using  
22 baited video cameras. *ICES J Mar Sci* 59:370-379
- 23 Collins MA, Yau C, Nolan CP, Bagley PM, Priede IG (1999b) Behavioural observations  
24 on the scavenging fauna of the Patagonian slope. *J Mar Biol Assoc UK* 79:963-  
25 970
- 26 Dayton PK, Hessler RR (1972) Role of biological disturbance in maintaining diversity in  
27 the deep-sea. *Deep-Sea Res* 19:199-208
- 28 Desbruyères D, Biscoito M, Caprais J-C, Colaço A, Comtet T, Crassous P, Fouquet Y,  
29 Khripounoff A, Le Bris N, Olu K, Riso R, Sarradin P-M, Segonzac M,  
30 Vangriesheim A (2001) Variations in deep-sea hydrothermal vent communities on  
31 the Mid-Atlantic Ridge near the Azores plateau. *Deep-Sea Res I* 48:1325-1346
- 32 Drazen JC (2002) A seasonal analysis of the nutritional condition of deep-sea macrourid  
33 fishes in the north-east Pacific. *J Fish Biol* 60:1280-1295
- 34 Ewing M, Worzel JL, Vine AC (1967) Early development of ocean-bottom photography  
35 at Woods Hole Oceanographic Institution and Lamont Geological Observatory.  
36 In: JB H (ed) *Deep-Sea Photography*. The Johns Hopkins Press, Baltimore, p 13-  
37 41
- 38 Fossen I, Cotton CF, Bergstad OA, Dyb JE (in press) Species composition and  
39 distribution patterns of fishes captured by longlines on the mid-Atlantic Ridge.  
40 *Deep-Sea Res II*
- 41 Fossen I, Cotton CF, Bergstad OA, Dyb JE (submitted) Species composition and  
42 distribution patterns of fishes captured by longlines on the mid-Atlantic Ridge.  
43 *Deep-Sea Res II*
- 44 Grassle JF, Sanders HL (1973) Life histories and the role of disturbance. *Deep-Sea Res*  
45 20:643-659

- 1 Grassle JFH, Sanders HL, Hessler RR, Rowe GT, McLellan T (1975) Pattern and  
2 zonation- a study of bathyal megafauna using the research submersible Alvin.  
3 Deep-Sea Res 22:457-481
- 4 Heezen BC, Hollister CD (1971) The Face of the Deep, Vol. Oxford University Press,  
5 Oxford
- 6 Heger A, King NJ, Wigham BD, Jamieson AJ, Bagley PM, Allan L, Pfannkuche O,  
7 Priede IG (in press) Benthic Bioluminescence in the bathyal North East Atlantic:  
8 Luminescent responses of *Vargula norvegica* (Ostracoda: Myodocopida) to  
9 predation by the deep water eel (*Synphobranchus kaupii*). Mar Biol DOI  
10 10.1007/s00227-006-0587-7
- 11 Henriques C, Priede IG, Bagley PM (2002) Baited camera observations of deep-sea  
12 demersal fishes of the northeast Atlantic Ocean at 15-28°N off West Africa. Mar  
13 Biol 141:307-314
- 14 Hessler RR, Ingram CL, Yayanos AA, Burnett BR (1978) Scavenging Amphipods from  
15 the floor of the Philippine trench. Deep-Sea Res 25:1029
- 16 Isaacs JD (1969) The nature of oceanic life. Scientific American 211:146-162
- 17 Isaacs JD, Schwartzlose RA (1975) Active animals of the deep-sea floor. Scientific  
18 American 233:85-91
- 19 Jamieson AJ (2004) Autonomous lander technology for biological research at mid-water,  
20 abyssal and hadal depths., University of Aberdeen, Aberdeen
- 21 Jamieson AJ, Bailey DM, Wagner H-J, Bagley PM, Priede IG (2006) Behavioural  
22 responses to structures on the seafloor by the deep-sea fish *Coryphaenoides*  
23 *armatus*: Implications for the use of baited landers. Deep-Sea Res I 53:1157-1166
- 24 Janßen F, Treude T, Witte U (2000) Scavenger assemblages under different trophic  
25 conditions: a case study in the deep Arabian Sea. Deep-Sea Res II 47:2999-3026
- 26 Jones EG (1999) "Burial at sea"; consumption and dispersal of large fish and cetacean  
27 food-falls by deep-sea scavengers in the Northeast Atlantic Ocean and Eastern  
28 Mediterranean Sea. PhD Thesis, University of Aberdeen, Aberdeen
- 29 Jones EG, Collins MA, Bagley PM, Addison S, Priede IG (1998) The fate of cetacean  
30 carcasses in the deep-sea: observations on consumption rates and succession of  
31 scavenging species in the abyssal north-east Atlantic. Proc Roy Soc London B  
32 265:1119-1127
- 33 Jones EG, Tselepides A, Bagley PM, Collins MA, Priede IG (2003) Bathymetric  
34 distribution of some benthic and benthopelagic species attracted to baited cameras  
35 and traps in the eastern Mediterranean. Mar Ecol Prog Ser 251:75-86
- 36 Kaufmann RS, Smith KL (1997) Activity patterns of mobile epibenthic megafauna at an  
37 abyssal site in the eastern North Pacific: Results from a 17-month time-lapse  
38 photographic study. Deep-Sea Res I 44:559-579
- 39 Kemp KM, Jamieson AJ, Bagley PM, Collins MA, Priede IG (in press) A new technique  
40 for sequential periodic bait-release at a camera platform in the deep sea; trial at  
41 3664m depth in the Charlie Gibbs Fracture Zone, Mid-Atlantic Ridge. Deep-Sea  
42 Res I
- 43 Kemp KM, Jamieson AJ, Bagley PM, McGrath H, Bailey DM, Collins MA, Priede IG  
44 (2006) Consumption of a large bathyal food fall, a six month study in the north-  
45 east Atlantic. Mar Ecol Prog Ser 310:65-76

- 1 King NJ (2006) Deep-sea demersal ichthyofauna of contrasting localities: Mid-Atlantic  
2 Ridge, Nazaré Canyon (North Atlantic Ocean) and Crozet Plateau (Southern  
3 Indian Ocean), with special reference to the abyssal grenadier, *Coryphaenoides*  
4 (*Nematonurus*) *armatus* (Hector, 1875), PhD Thesis, University of Aberdeen,  
5 Aberdeen
- 6 King NJ, Bagley PM, Priede IG (2006) Depth zonation and latitudinal distribution of  
7 deep-sea scavenging demersal fishes of the Mid-Atlantic Ridge, 42 to 53°N. *Mar*  
8 *Ecol Prog Ser* 319:263-274
- 9 Klages M, Muyakshin S, Soltwedel T, Arntz WE (2002) Mechanoreception, a possible  
10 mechanism for food fall detection in deep-sea scavengers. *Deep-Sea Res I*  
11 49:143-155
- 12 Klages M, Vopel K, Bluhm H, Brey T, Soltwedel T, Arntz WE (2001) Deep-sea food  
13 falls: first observation of a natural event in the Arctic Ocean. *Polar Biol* 24:292-  
14 295
- 15 Lampitt RS, Burnham MP (1983) A Free-Fall Time-Lapse Camera and Current-Meter  
16 System Bathysnap with Notes on the Foraging Behavior of a Bathyal Decapod  
17 Shrimp. *Deep-Sea Res A* 30:1009-1017
- 18 Lampitt RS, Merrett N, Thurston MN (1983) Inter-relations of necrophagus amphipods, a  
19 fish predator and tidal currents in the open sea. *Mar Biol* 74:73-78
- 20 Laver MB, Olsson MS, Endelman JL, Smith KL (1985) Swimming rates of scavenging  
21 deep-sea amphipods recorded with a free-vehicle video camera. *Deep-Sea Res I*  
22 32:1135-1142
- 23 Lawson GS, Tyler PA, Young CM (1993) Attraction of deep-sea amphipods to  
24 macrophyte food falls. *J Exp Mar Biol Ecol* 169:33-39
- 25 Merrett NR (1987) A zone of faunal change in assemblages of abyssal demersal fish in  
26 the eastern North Atlantic: a response to seasonality in production? *Biol Oceanog*  
27 5:137-151
- 28 Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes.  
29 *Philos Trans R Soc London [B]* 360:13-20
- 30 Premke K, Muyakshin S, Klages M, Wegner J (2003) Evidence for long-range  
31 chemoreceptive tracking of food odour in deep-sea scavengers by scanning sonar  
32 data. *J Exp Mar Biol Ecol* 285-286:283-294
- 33 Priede IG, Bagley PM (2000) *In situ* studies on deep-sea demersal fishes using  
34 autonomous unmanned lander platforms. *Oceanog Mar Biol Ann Rev* 38:357-392
- 35 Priede IG, Bagley PM, Armstrong JD, Smith KL, Merrett NR (1991) Direct measurement  
36 of active dispersal of food-falls by deep-sea demersal fishes. *Nature* 351:647-649
- 37 Priede IG, Bagley PM, Smith A, Creasey S, Merrett NR (1994a) Scavenging deep  
38 demersal fishes of the Porcupine Seabight, North-east Atlantic: Observations by  
39 baited camera, trap and trawl. *J Mar Biol Assoc UK* 74:481-498
- 40 Priede IG, Bagley PM, Smith KL (1994b) Seasonal change in activity of abyssal  
41 demersal scavenging grenadiers *Coryphaenoides* (*Nematonurus*) *armatus* in the  
42 eastern Pacific Ocean. *Limnol Oceanog* 39:279-285
- 43 Priede IG, Deary AR, Bailey DM, Smith KL (2003) Low activity and seasonal change in  
44 population size structure of grenadiers in the oligotrophic abyssal Central North  
45 Pacific Ocean. *J Fish Biol* 63:187-196

- 1 Priede IG, Froese R, Bailey DM, Bergstad OA, Collins MA, Dyb JE, Henriques C, Jones  
2 EG, King N (2006) The absence of sharks from abyssal regions of the world's  
3 oceans. Proc R Soc London B 273:1435-1441
- 4 Priede IG, Merrett NR (1996) Estimation of abundance of abyssal demersal fishes; a  
5 comparison of data from trawls and baited cameras. J Fish Biol 49:207-216
- 6 Priede IG, Smith KL (1986) Behaviour of the abyssal grenadier *Coryphanoides yaquinae*,  
7 monitored using ingestible acoustic transmitters in the Pacific Ocean. J Fish Biol  
8 29:199-206
- 9 Priede IG, Smith KL, Armstrong JD (1990) Foraging behaviour of abyssal grenadier fish:  
10 inferences from acoustic tagging and tracking in the North Pacific Ocean. Deep-  
11 Sea Res 37:81-101
- 12 Rose CS, Stoner AW, Matteson K (2005) Use of high-frequency imaging sonar to  
13 observe fish behaviour near baited fishing gears. Fish Res 76:291-304
- 14 Sainte-Marie B, Hargrave BT (1987) Estimation of scavenger abundance and distance of  
15 attraction to bait. Mar Biol 94:431-443
- 16 Seibel BA, Drazen JC (in press) The rate of metabolism in marine animals:  
17 Environmental constraints, ecological demands and energetic opportunities. Philos  
18 Trans R Soc London [B]
- 19 Smith A, Priede IG, Bagley PM, Addison SW (1997a) Interception and dispersal of  
20 artificial foodfalls by scavenging fishes in the abyssal Northeast Atlantic: early-  
21 season observations prior to annual deposition of phytodetritus. Mar Biol  
22 128:329-336
- 23 Smith CR (1985) Food for the deep sea: utilization, dispersal and flux of nekton falls at  
24 the Santa Catalina Basin floor. Deep-Sea Res 32:417-442
- 25 Smith CR, Baco AR (2003) Ecology of whale falls at the deep-sea floor. Oceanogr Mar  
26 Biol Annu Rev 41:311-354
- 27 Smith CR, Berelson W, Demaster DJ, Dobbs FC, Hammond D, Hoover DJ, Pope RH,  
28 Stephens M (1997b) Latitudinal variations in benthic processes in the abyssal  
29 equatorial Pacific: control by biogenic particle flux Deep-Sea Res II 44:2295-  
30 2317
- 31 Smith CR, Kukert H, Wheatcroft RA, Jumars PA (1989a) Vent fauna on whale remains.  
32 Nature 341:27-28
- 33 Smith KL, Alexandrou D, Edelman JR (1989b) Acoustic detection and tracking of  
34 abyssopelagic animals: description of an autonomous split-beam acoustic array.  
35 Deep-Sea Res 36:1427-1441
- 36 Stockton WL, DeLaca TE (1982) Food falls in the deep-sea: occurrence, quality and  
37 significance. Deep-Sea Res 29:157-169
- 38 Tamburri MN, Peltzer ET, Freiderich GE, Aya I, Yamane K, Brewer PG (2000) A field  
39 study of the effects of CO<sub>2</sub> ocean disposal on mobile deep-sea animals. Mar Chem  
40 72:95-101
- 41 Trenkel VM, Lorange P, Mahévas S (2004) Do visual transects provide true population  
42 density estimates for deepwater fish? ICES J Mar Sci 61:1050-1056
- 43 Wagner H-J (2003) Volumetric analysis of brain areas indicates a shift in sensory  
44 orientation during development in the deep-sea grenadier *Coryphaenoides*  
45 *armatus*. Mar Biol 142:791-797

1 Widder EA, Robison BH, Reisenbichler KR, Haddock SHD (2005) Using red light for in  
2 situ observations of deep-sea fishes. *Deep-Sea Res I* 52:2077-2085  
3 Wilson RR, Smith KL (1984) Effect of near-bottom currents on detection of bait by the  
4 abyssal grenadier fishes *Coryphaenoides* spp., recorded in situ with a video  
5 camera on a free fall vehicle. *Mar Biol* 84:83-91  
6 Wilson RR, Waples RS (1983) Distribution, morphology, and biochemical genetics of  
7 *Coryphaenoides armatus* and *Coryphaenoides yaquinae* (Pisces, Macrouridae) in  
8 the central and eastern North Pacific. *Deep-Sea Res* 30:1127-1145  
9 Witte U (1999) Consumption of large carcasses by scavenger assemblages in the deep  
10 Arabian Sea: observations by baited camera. *Mar Ecol Prog Ser* 183:139-147  
11 Yau C, Priede IG, Collins MA (2000) Estimation of the abundance of deep-sea fishes:  
12 telemetry and the problem of measuring swimming speed. In: Moore A, Russell I  
13 (eds) *Advances in fish telemetry Proceedings of the third conference on fish*  
14 *telemetry in Europe (Norwich, June 1999)*. MAFF, Lowestoft, p 159-164  
15  
16



1 Table 1. Examples of the advantages and disadvantages of various gears for the  
 2 assessment of animal biodiversity, abundance and biomass in benthic deep-water  
 3 systems.

4

<b>Survey gear</b>	<b>Advantages</b>	<b>Disadvantages</b>
Baited camera	Small sea time requirement for long observation. Deployment and recovery possible from smaller vessels, with non-specialist crews and equipment. Provides behavioral data on scavengers. Relatively non-destructive.	Lack of standardization. Many assumptions in abundance estimates. Some taxa/size ranges do not come to bait. Animals may be difficult to identify to species from images. Expensive to build equipment. Relatively high chance of loss of equipment. Weights of animals cannot be determined directly, and require length/weight relationships from captured specimens.
Bottom trawling	Obtains voucher specimens. Abundance and biomass estimates relatively simple. Historical datasets available for comparison.	Destructive. Time on bottom difficult to determine at depth, making abundance estimates less precise. On rougher ground some nets fish poorly or will be damaged. Ship cannot do other work while fishing. Net avoidance varies between net types and taxa. Few ships and individuals have the ability to trawl to abyssal depths.
ROV/ submersible survey	Some ability to obtain voucher specimens. High-quality video and stills cameras available.	Ship cannot do other work while dive underway. Camera avoidance varies between taxa. Field of view and angle of line of sight vary between and during surveys.
Camera sled survey	Highly standardized results. Easy to tell whether camera was on the bottom. Relatively non-destructive.	Ship cannot do other work while tow underway. Camera avoidance varies between taxa. Difficult to estimate sizes of animals which are not on the bottom, unless stereo cameras are used.

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**Table 2. A selection of key baited camera systems and deployments in the deep-ocean**

<b>Year</b>	<b>System name</b>	<b>Location(s)</b>	<b>Key result</b>	<b>Reference</b>
1969 - 1975	Monster camera	Pacific, Indian and Antarctic Oceans, Mediterranean	First observations. Differences between ocean basins described.	Isaacs 1969 Heezen & Hollister 1971 (Isaacs & Schwartzlose 1975)
1981	Bathysnack (baited version of Bathysnap)	North Atlantic	Establishment of latitudinal patterns in scavenger distribution.	Thurston et al. 1995
1983	Scripps Free Vehicle Video (FVV)	North Pacific	Video recordings reveal swimming speeds and approach directions of scavengers.	Wilson and Smith, 1984 Laver et al 1985
1986-2006	Acoustic Tracking Experiment (ATEX) and Aberdeen University Deep Ocean Submersible (AUDOS), Robust Biodiversity lander (ROBIO)	North Atlantic and North Pacific Southern Indian Ocean	Acoustic tracking of abyssal fishes provides detailed information about the behavior of fishes. Deepest fishes recorded at baited lander 5900 m CNP. Commercial use of baited camera in the deep-ocean.	(Bagley et al. 1994) Henriques 2004 Priede et al. 1990
1978, 1989	“autonomous instrument carriers” lowered by wire	Philippine, Chile and Mariana Trenches	Deepest baited camera deployments (>10000 m) observe only crustaceans, and no fishes.	Hessler et al. 1978 Beliaev 1989
1998, 2001-6	Large Abyssal Food Fall (LAFF) and Deep-Ocean Benthic Observer (DOBO) landers	North Atlantic	Marine mammal deployment reveals temporal succession and interactions between scavenging species. Periodic bait release system developed.	(Jones et al. 1998) Kemp et al. 2006 Kemp et al. 2006 submitted
2005	Eye in the sea	Gulf of Mexico	Red light illumination and electronic jellyfish	Widder et al. 2005

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1 **Figures**

2 Figure 1. The Monster Camera (photo courtesy of Scripps Institution of Oceanography Library).

3 In this image the camera housing is inverted at bottom right, and strobe at top left. The system

4 was deployed with the camera facing down, towards a perforated metal can containing the bait.

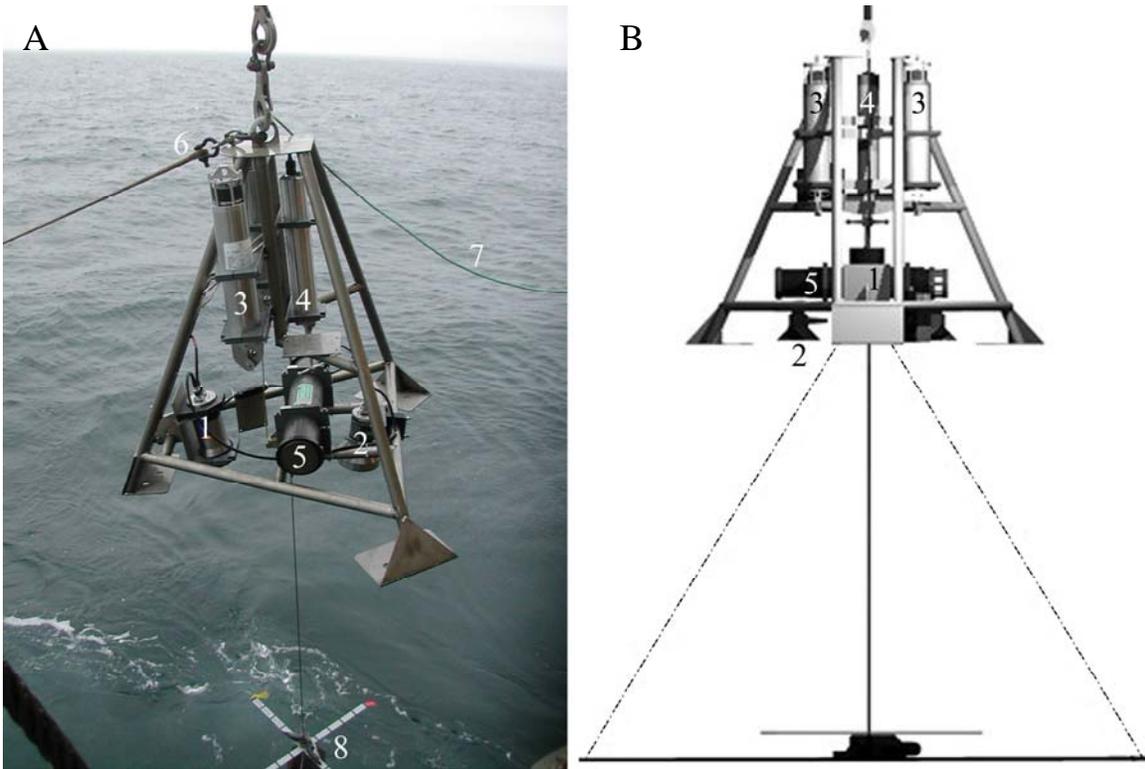
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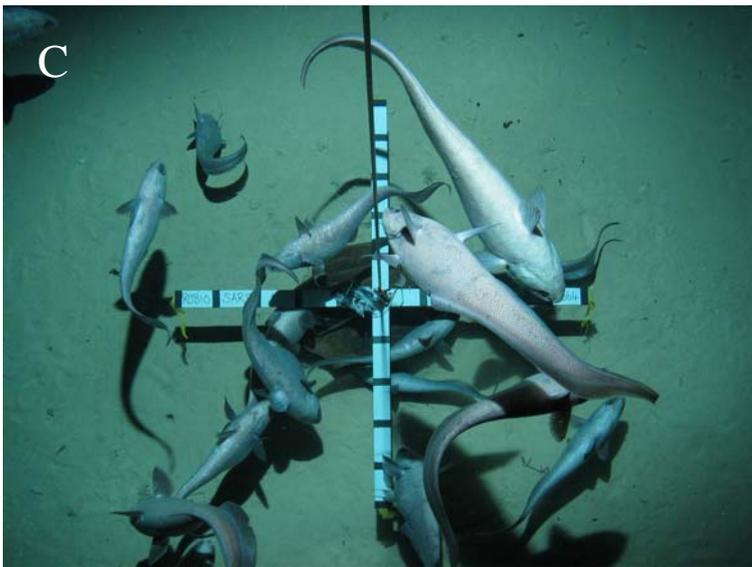
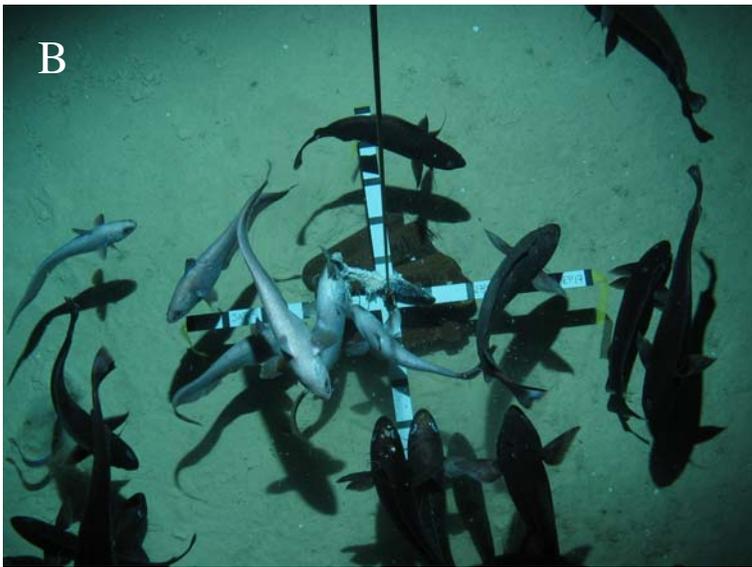
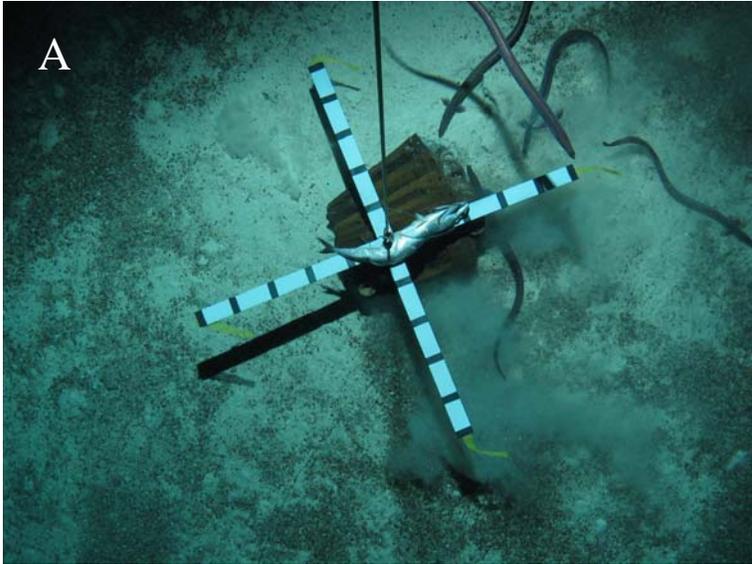
1 Figure 2 The ROBIO lander, the latest version of the ATEX/AUDOS family of baited landers,  
2 being deployed in tethered mode; A) Photograph of ROBIO being deployed on the MAR; B)  
3 diagrammatic representation (AutoCAD) of ROBIO in tethered mode. The lander consists of a  
4 grade-2 titanium frame with a digital camera (1), flash unit (2), acoustic releases (3), current  
5 meter (4; in these images a Sontek current meter), battery housing and rechargeable battery,  
6 and 2 m wire stop with bait, reference cross and ballast (8). The link with the mooring line (6)  
7 and quick release line are visible (7) in Fig 2A. The dashed lines in Fig 2B indicate the field of  
8 view of the camera.

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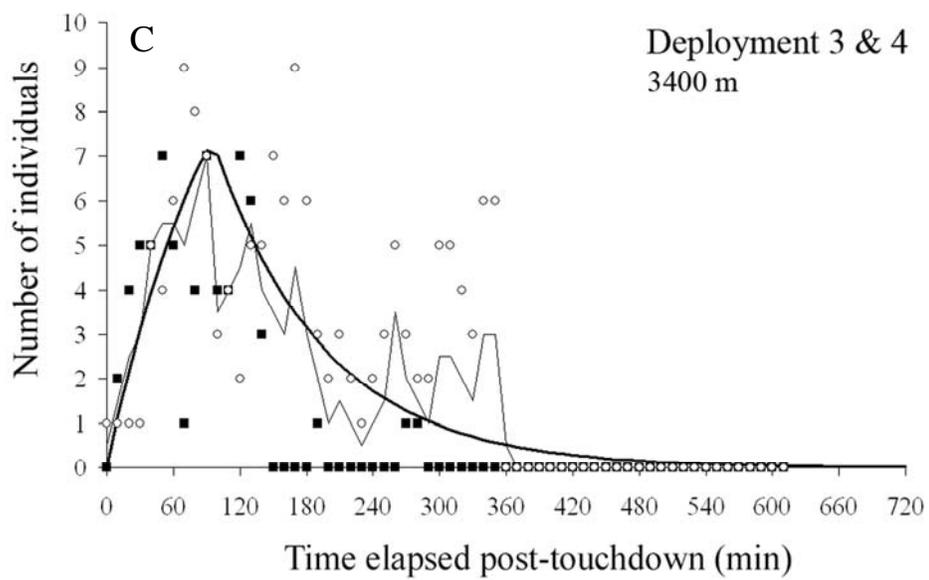
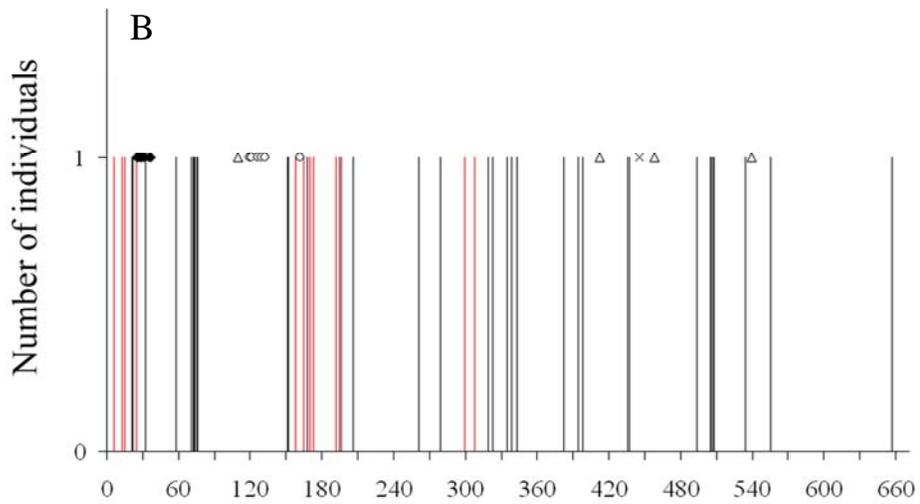
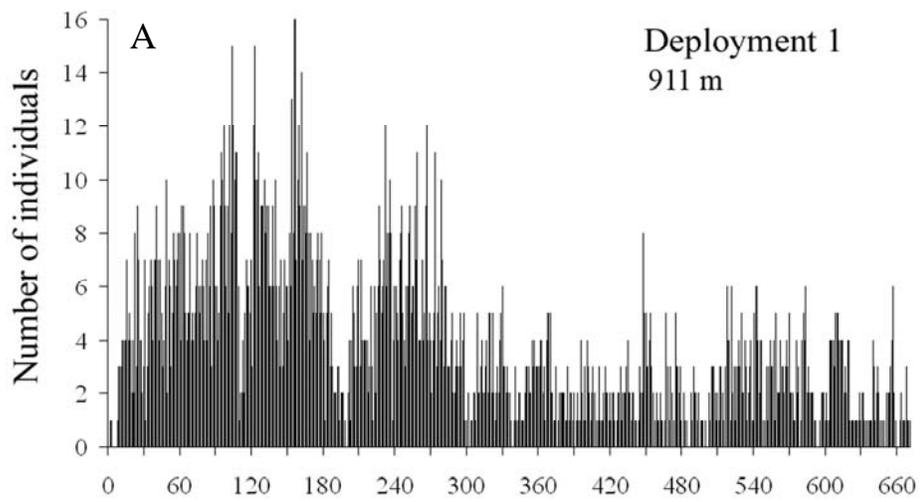
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1 Figure 3. Images collected by the ROBIO baited camera system on the Mid-Atlantic Ridge, July  
2 2004. The fishes photographed are the dominant scavenging vertebrates in their respective depth  
3 zones. Reference bars are marked in 10 cm increments, bait is a single Atlantic mackerel.  
4 Identifications are based on morphometric measurements from the images, and using specimens  
5 trawled from nearby areas. A) eels, *Synaphobranchus* sp. at 1569 m, 42° 50'N, 29° 29'W, B)  
6 morid *Antimora rostrata* (black) and grenadiers *Coryphaenoides armatus* (gray) at 2355 m, 53°  
7 17' N, 35° 30' W. C) *C. armatus* at 3346 m, 51° 34'N, 31° 02' W. Note the larger size of the  
8 grenadiers in this abyssal image.  
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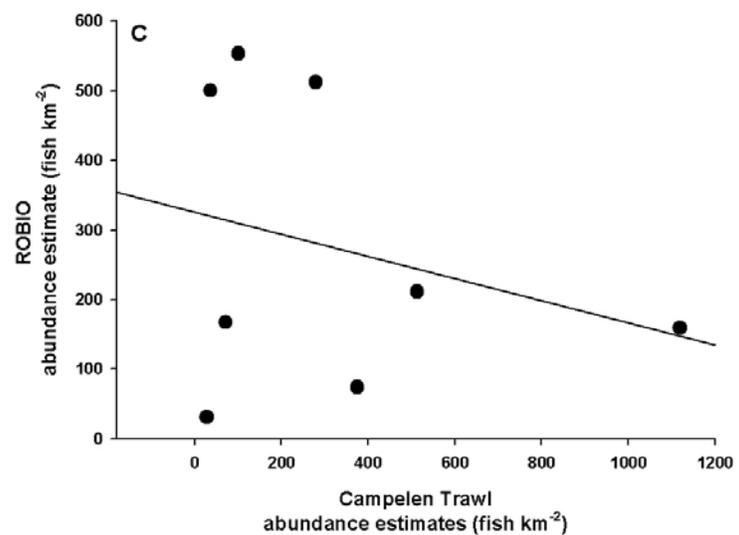
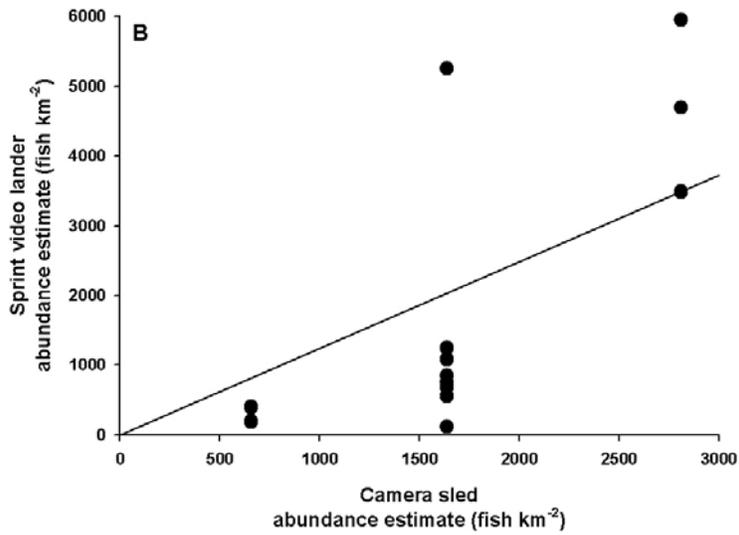
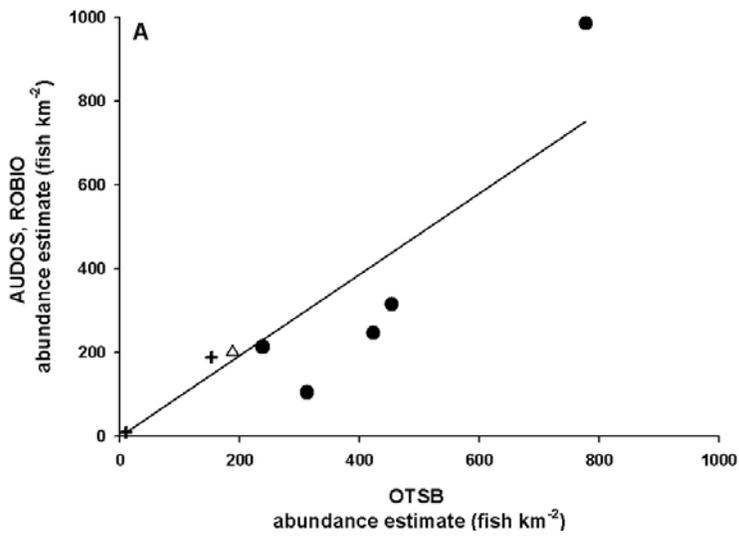


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1 **Figure 4** Numbers of fish within view of the camera over time after touchdown at 911 m,  
2 Nazaré Canyon, Portuguese coast (A and B). Each vertical histogram bar represents one  
3 image frame with fish visible. The top panel (A) indicates data for *Synaphobranchus*  
4 spp., the bottom panel (B) for the other taxa recorded. The most common taxa attending  
5 bait are indicated by solid bars; black bars indicate *Mora moro*, red bars *Trachyrincus*  
6 *scabrus?*. Less common visitation is marked by symbols; crosses indicate *Hexanchus*  
7 *griseus?*, open circles *Deania* sp., open triangles, unidentified sharks, and black solid  
8 diamonds *Phycis* sp. The bait was not completely consumed during the deployment. C)  
9 Numbers of *Coryphaenoides armatus* as a function of time (max number per 10 min  
10 interval) at 3400 m, Nazaré Canyon. Raw deployment data is represented by open circles  
11 and closed squares. The mean number of individuals for the two deployments is  
12 represented by the thin black line and the smoothed “shark’s fin” model fitted values  
13 (Priede et al. 1990) by the thick black line.  
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1 Figure 5 Comparison of abundance estimates from towed gears and baited cameras, obtained at  
2 the same locations and weeks. Lines and the formulae below are least squares regression fits;  
3 Spearman correlations were used to determine the strength of the relationships. A) OTSB trawls  
4 in the Porcupine Seabight (solid circles), Porcupine Abyssal Plain (averages of several trawls,  
5 crosses) and Crozet Island (open triangle), plotted against AUDOS/ROBIO data ( $y=0.97x$ ,  
6 correlation coefficient = 0.86,  $P = 0.01$ ,  $n = 8$ ). B) Camera sled data from the North Pacific (solid  
7 circles), plotted against Sprint video lander abundances estimates. ( $y=1.24x$ , correlation  
8 coefficient = 0.62,  $P = 0.02$ ,  $n = 14$ ). C) Campelen trawls on the Mid-Atlantic Ridge, plotted  
9 against ROBIO data ( $y=-0.15x$ , correlation coefficient = 0.02,  $P = 0.96$ ,  $n = 8$ ). Note that in  
10 Panels A and C the variation in abundance is due to spatial separation, whereas in Panel B the  
11 lander and camera sled estimates are all at the same location, but the pairs took place over a  
12 period of 15 years.  
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